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Evidence for an extinct lineage of angiosperms from the Early Cretaceous of Patagonia and implications for the early radiation of flowering plants

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Summary

- The pinnately lobed Aptian leaf fossil *Mesodescolea plicata* was originally described as a cycad, but new evidence from cuticle structure suggests it is an angiosperm. Here we document the morphology and cuticle anatomy of *Mesodescolea* and explore its significance for early angiosperm evolution.
- We observed macrofossils and cuticles of *Mesodescolea* with light microscopy, SEM, and TEM and used phylogenetic methods to test its relationships among extant angiosperms.
- *Mesodescolea* has chloranthoid teeth and tertiary veins forming elongate areoles. Its cuticular morphology and ultrastructure reject cycadalean affinities, while its guard cell shape and stomatal ledges are angiospermous. It shares variable stomatal complexes and epidermal oil cells with angiosperm leaves from the lower Potomac Group. Phylogenetic analyses and hypothesis testing support its placement within the basal ANITA grade, most likely in Austrobaileyales, but it diverges markedly in leaf form and venation.
- Whereas many Early Cretaceous angiosperms fall within the morphological range of extant taxa, *Mesodescolea* reveals unexpected early morphological and ecophysiological trends. Its similarity to other Early Cretaceous lobate leaves, many previously identified as eudicots but in some cases predating the appearance of tricolpate pollen, may indicate that *Mesodescolea* is part of a larger extinct lineage of angiosperms.

Key words: Aptian, Argentina, cuticle, leaves, Mesozoic, paleobotany, stomata.

Introduction

The origin and initial radiation of the angiosperms represent pivotal events in the origin of the Earth's present biota. Although the time of origin of flowering plants (i.e. the age of the most recent common ancestor of all extant species) is hotly debated (Smith *et al.*, 2010; Doyle, 2012; Beaulieu *et al.*, 2015; Magallón *et al.*, 2015; Herendeen *et al.*, 2017; Barba-Montoya *et al.*, 2018; Coiro *et al.*, 2019; Li *et al.*, 2019), it is undeniable that the Early Cretaceous was a critically important period for the expansion and the radiation of angiosperm morphology (Doyle, 1969; Muller, 1970; Hickey & Doyle, 1977; Lupia, 1999; Friis *et al.*, 2011; Coiro *et al.*, 2019; Donoghue, 2019). It has been postulated that this expansion corresponds largely to the radiation of the vast mesangiosperm clade, which includes 99.9% of living angiosperm species (Doyle, 2012; Magallón *et al.*, 2018). The remaining basal lineages of angiosperms, which form the informal ANITA (or ANA) grade (*Amborella*, Nymphaeales, Austrobaileyales), are nowadays extremely depauperate in species, suggesting either no major radiation in the earliest phases of angiosperm history (Soltis *et al.*, 2019), possibly due to ecophysiological and geographic restriction to wet understory habitats (Feild *et al.*, 2004), or extensive extinction of other ancient lines. The latter scenario might imply that efforts to reconstruct the early evolutionary history of angiosperms from extant data alone might miss crucial details in terms of both diversification dynamics and trait evolution (Marshall, 2017).

Fortunately, the Early Cretaceous fossil record offers some insights on the early radiation of angiosperms (see Fig. 1 for stratigraphic subdivisions). Many Early Cretaceous fossils, especially flowers with pollen in the stamens or on the stigma (Friis *et al.*, 2011), have been associated with extant angiosperm clades by phylogenetic analyses (e.g. Doyle *et al.*, 2008; Friis *et al.*, 2009; Doyle & Endress, 2010, 2014). These studies have typically analyzed morphological data on extant and fossil taxa while assuming relationships among extant taxa based mainly on molecular data. A few fossils have been assigned to the basal ANITA grade, particularly Nymphaeales, which deviate ecologically from the other two ANITA lines in being aquatic herbs and might have escaped any ancestral ecological constraints. However, most have been placed at positions fairly low in the mesangiosperm clade: among Chloranthaceae, several lines of magnoliids, and basal monocots and eudicots. Most of these fossils fall within the morphological spectrum of extant angiosperms, suggesting either limited morphological exploration during the early phases of the Cretaceous expansion or a bias against the description of taxa of unclear affinities (Sauquet &

Magallón, 2018). Perhaps the most conspicuous exceptions are the bizarre aquatic plants *Archaefructus* and *Montsechia* from the Barremian of China and Spain, respectively (Sun *et al.*, 2002; Gomez *et al.*, 2015). *Montsechia* has been linked with extant *Ceratophyllum* (Gomez *et al.*, 2015), but *Archaefructus* has resisted phylogenetic placement (Doyle & Endress, 2014).

The fossils treated in this paper appear to be another major exception. *Mesodescolea* was first described by Archangelsky (1963) from the Anfiteatro de Ticó Formation, the lowest of three units making up the Baqueró Group in southern Argentina (Fig. 1), and later found in the uppermost unit, the Punta del Barco Formation (Archangelsky, 2001). Both formations are dated radiometrically as late Aptian (*c.* 114.7–118.6 Ma: Limarino *et al.*, 2012). The associated plant assemblage contains diverse ferns, 'seed ferns', cycads, Bennettitales, Ginkgoales, and conifers (Del Fueyo *et al.*, 2007; Llorens *et al.,* 2020). These and correlative units elsewhere in Argentina provide the first records of angiosperm leaves in southern South America (Romero & Archangelsky, 1986; Puebla, 2009; Archangelsky *et al.*, 2009; Romero *et al.*, 2016), together with reticulate-columellar monosulcate angiosperm pollen, which extends back into the Barremian (Archangelsky *et al.*, 2009; Archangelsky & Archangelsky, 2013; Llorens & Perez Loinaze, 2016). This region was part of the Southern Gondwana floral province of Brenner (1976). *Mesodescolea* was originally described as having bipinnate leaves and was compared with the cycad genera *Stangeria* (extant) and *Ctenis* (fossil). Subsequently, Archangelsky & Petriella (1971) described the venation in more detail, and Artabe & Archangelsky (1992) used SEM to characterize the epidermal structure. A close relationship of *Mesodescolea* and *Stangeria* was also supported by morphological cladistic analyses of extant and fossil cycads (Hermsen *et al.*, 2006; Martínez *et al.*, 2012; Coiro & Pott, 2017), but these analyses did not consider or test the possibility of non-cycadalean affinities.

During a phylogenetic survey of extant and fossil cycads, we recognized that the epidermal anatomy of *Mesodescolea* tells a very different story. In this article, we show that *Mesodescolea* does not have the typical leaf architectural and epidermal characters of the Cycadales, and instead shows many characters that support an angiosperm affinity. It also shares special epidermal features with some of the oldest Cretaceous angiosperm leaves, from the lower Potomac Group of Virginia, USA (Upchurch, 1984a,b), of Aptian and early Albian age (Doyle & Endress, 2014; Doyle & Upchurch, 2014; Tanrikulu *et al.*, 2018), although it has very different leaf architecture.

Furthermore, our phylogenetic analyses suggest it represents a highly divergent line in the basal ANITA grade.

These results may be of broader significance because *Mesodescolea* shows similarities to other pinnately and ternately lobed Cretaceous leaves, some of which have been compared with the basal eudicot order Ranunculales (Vakhrameev & Krassilov, 1979; Doyle, 2001; Krassilov & Volynets, 2008; Jud & Hickey, 2013; Jud, 2015; Golovneva *et al.*, 2018). This raises the possibility that *Mesodescolea* is just one member of a major extinct clade of early angiosperms whose existence was not previously suspected, thus painting a significantly modified picture of patterns of morphological evolution in the early radiation of angiosperms. Its unusual venation also suggests unexpected reversals of ecophysiological innovations that have been associated with the ecological success of angiosperms (Boyce *et al.*, 2009; Feild *et al.*, 2011).

Materials and Methods

Fossil specimens investigated

The specimens investigated for this revision include leaves and slides from the Natural History Museum in London (NHM) that were prepared by Archangelsky and used to first describe the species (Archangelsky, 1963), and specimens from the Museo de La Plata in La Plata, Argentina (LPPB). The original collections from the Anfiteatro de Ticó Formation of the Baqueró Group come from section SP4 of Archangelsky (2001), also called the *Ticoa harrisii* fossiliferous level, which was deposited in fluvial environments. *Mesodescolea* is a relatively abundant fossil in one of the layers at this fossil site. Its principal associates are *Ruflorinia/Ktalenia* (a presumed 'seed fern') and the conifer *Araucarites baqueroensis.* Archangelsky (1967) noted that the specimens in this layer show little evidence of transport and could have been deposited almost *in situ*. All specimens observed are listed in Table S1.

Light microscopy and image analysis of fossil material

Fossil slides were observed using a Nikon Eclipse LV100ND microscope. Confocal observations were made using a Nikon A1-Si laser-scanning confocal microscope, with two excitation lines: 488-nm line of 50-mW sapphire laser (Coherent Inc.), and 561-nm line of 50-mW sapphire laser (Coherent Inc.). Autofluorescence signal was collected with two photomultiplier detectors with the

following wavelength emission windows: 500–550 nm for the 488-nm laser, 570–620 nm for the 561-nm laser. Measurements on the pictures were obtained using ImageJ (Abràmoff *et al.*, 2004).

TEM of fossil material

Well-preserved cuticular fragments from leaf macrofossils (LPPB 5126 b) were manually separated from the bedding plane and cleaned with dilute sodium hypochlorite. The cuticle fragments were processed, cut and mounted following the techniques outlined by Archangelsky *et al.* (1986). Observations were made on a Zeiss EM 109 microscope at the Electron Microscopy Service of the Cellular Biology Department, Faculty of Medicine, Buenos Aires University. Preparations are deposited at the Palaeobotanical Collection of the Argentine Museum of Natural Sciences 'Bernardino Rivadavia' under the designation BA Pb MET-103. The terminology used here to describe cuticular membranes follows Archangelsky *et al*. (1986) and Guignard (2019).

Extant material

Cuticular material from *Stangeria* and extant angiosperms was obtained from various sources. Specimens from the Zurich Herbarium (Z) provided important information on Ranunculales and other basal eudicots. Materials from the Texas State University and Florida State Museum collections of extant angiosperm leaf cuticles provided data on ANITA lineages, Chloranthales, magnoliids, and basal eudicots. Illustrations in published literature and M.S./Ph.D. theses provided information on monocots and taxa not represented in the Texas and Florida collections. We made observations concerning the leaf architecture of extant angiosperm taxa on the Jack Wolfe collection of cleared leaves at the Smithsonian Institution (mostly images housed in the Texas State University paleobotanical collections) and herbarium specimens at Kew (K), Paris (P), and the University of California Davis (DAV). The observations on Kew and Paris material were used previously by Eklund *et al.* (2004). Additional materials and methods are described in Methods S1.

Phylogenetic analyses

The placement of *Mesodescolea* within the angiosperms was tested using the matrix of Kvaček *et al.* (2016), trimmed to include only leaf characters and updated by addition of seven new characters (orders of reticulate venation, shape of tertiary vein areas, freely ending veinlets, intramarginal or fimbrial vein, Zone I-type stomatal variation, T-pieces, and intrusive epidermal

oil cells) and rescoring of a few taxa (for further details see Notes S1). We employed Maximum Parsimony (MP) and Bayesian Inference (BI) to place *Mesodescolea* on three backbone trees, which differ in the arrangement of the five mesangiosperm clades. Relationships within these clades follow Endress & Doyle (2009), based on the combined morphological and molecular (18S nrDNA, *rbcL*, *atpB*) analysis of Doyle & Endress (2000), with modifications incorporating more recent molecular results. In the D&E tree, with the mesangiosperm clades arranged as in Endress & Doyle (2009), Chloranthaceae and *Ceratophyllum* form a clade sister to the remaining mesangiosperms, in which eudicots are sister to magnoliids and monocots. In the J/M tree, with the arrangement of mesangiosperm clades found in analyses of whole plastid genome sequences by Jansen *et al.* (2007) and Moore *et al.* (2007), Chloranthaceae and magnoliids form a clade sister to the remaining mesangiosperms, and *Ceratophyllum* is sister to the eudicots. In the Li *et al.* tree (Li *et al.*, 2019, fig. 2, left), Chloranthaceae are sister to the remaining mesangiosperms and other clades are arranged as in the J/M tree.

Many terminal taxa in the Kvaček *et al*. (2016) data set are families, scored based on phylogenetic inference of ancestral states. This risks overlooking relationships to taxa nested within the families. However, when Aptian-Albian fossils can be related to these families, they appear to be stem relatives rather than crown group members. For example, *Walkeripollis* and *Virginianthus* are apparently related to but more plesiomorphic than Winteraceae and Calycanthaceae, respectively (Doyle & Endress, 2010). In some cases, there is evidence that the crown group was much younger than Aptian; e.g. Proteaceae are united by distinctive triporate pollen first known from the Cenomanian (Jardiné & Magloire, 1965; Ward & Doyle, 1994).

MP analyses were conducted using PAUP* ver. 4.0b10 (Swofford, 2003), using the three trees as backbone constraints. Search for the most parsimonious tree(s) was conducted using heuristic search with 500 replicates. The relative parsimony of all positions of *Mesodescolea* was also determined by moving the fossil manually to all branches using MacClade (Maddison & Maddison, 2003). Bootstrap analysis was conducted for 1000 replicates using a heuristic search strategy and adding *Mesodescolea* as the first taxon, with the option 'Multtrees' deactivated (i.e. keeping only one tree per replicate).

BI analyses were conducted using MrBayes ver. 3.2.6 (Ronquist *et al.*, 2012). The Mk_{var} model was employed. Two independent runs with four chains (one cold and three heated) were run

for 1,000,000 generations sampling every 100th generation. Consensus trees were obtained after removing the first 25% as burn-in.

Statistical support for placements of *Mesodescolea* with each of the various methods was summarized using RoguePlots (Klopfstein & Spasojevic, 2019), using the MP bootstrap replicates and the post burn-in combined runs from the BI analyses. Character support for various relationships under parsimony optimization was investigated with MacClade (Maddison & Maddison, 2003).

Phylogenetic hypothesis testing

To evaluate support for the placement of *Mesodescolea* in several alternative positions in the phylogeny of angiosperms, we also followed a hypothesis-testing approach. Eight positions were selected: with *Mesodescolea* sister to Austrobaileyales, to the clade of Austrobaileyales plus mesangiosperms, to mesangiosperms, to Chloranthaceae, to eudicots, to Ranunculales, to Papaveraceae, and to *Ceratophyllum*. The D&E, J/M, and Li *et al.* topologies were used as backbone trees for these different placements.

Bayesian topology testing was conducted using Bayes Factors (BFs) (Kass & Raftery, 1995). The marginal likelihood of a model is the conditional probability of the data given that model integrated over all possible values of the model parameters. Given that tree topology can be considered part of the model explaining the observed data, marginal likelihoods can be used in Bayesian topology testing via BFs. Using a fully constrained topology allows us to limit the prior tree space and thus avoid potential issues in the estimation and use of BFs (Bergsten *et al.*, 2013). Marginal likelihoods were obtained using Stepping-Stone sampling (SS) (Xie *et al.*, 2010) run on MrBayes ver. 3.2.6 as implemented on the CIPRES Science Gateway (Miller *et al.*, 2010). These analyses allow us to estimate the marginal likelihood for different models with better accuracy than other measures (e.g. harmonic mean estimator). The SS was run with four independent runs each with four chains, one cold and three heated. The chains were run for 1,100,000 generations sampling every 100th generation, using an alpha of 0.3 and 10 steps.

Results

Systematics

Spermatophyta

Angiospermae

Incertae sedis

Genus *Mesodescolea* S.Archang.

Species *Mesodescolea plicata* S.Archang. emend. S.Archang. & Petriella

Emended diagnosis: Leaves or pinnae of bipinnate leaves pinnately dissected, elliptical to oblong, with asymmetrical base and apex. Lobes alternate to subopposite, with broad base and acute apex. Base of the lobe with decurrent basal (basiscopic) and acute apical (acroscopic) margin, margins of the lobe sparsely serrated. Teeth with one medial vein and two lateral veins fusing below the apex (chloranthoid type). Major venation craspedodromous, with a single secondary vein entering the apical side of each lobe and running to the apex. Tertiary veins forming an irregular reticulum of elongated areoles, with no freely ending veinlets present.

Leaf with a stomatiferous and a non-stomatiferous side (presumably abaxial and adaxial, respectively). Non-stomatiferous cuticle with isodiametric, polygonal pavement cells, with anticlinal walls straight to slightly undulate. Outer surface of cuticle with irregularly arranged striations. Stomatiferous cuticle with isodiametric pavement cells between the veins and elongated pavement cells at the veins. Outer surface of cuticle with irregular striations between the veins and longitudinally arranged striations at the veins. Radiostriate idioblasts present.

Stomata oriented irregularly, with variable subsidiary cell arrangement, mostly laterocytic, with some paracytic and actinocytic complexes, some stomata with irregular features, such as subsidiary cells that do not extend the full length of the guard cells. Guard cell pairs slightly oval to circular, with T-shaped thickening of the inner cuticle at the poles, conspicuously thickened outer ledges forming an outer vestibulum. Cuticular striations usually radiating laterally and perpendicular to the guard cells.

Holotype: LIL PB 2548, Museo de Ciencias Naturales de la Fundación Miguel Lillo, San Miguel de Tucumán, Argentina.

Type locality: Estancia La Magdalena, Anfiteatro de Ticó, Santa Cruz Province, Argentina.

Type unit and age: Baqueró Group, Anfiteatro de Ticó Formation, *Ticoa harrisii* layer. Early Cretaceous (late Aptian).

Leaf morphology and venation

Most specimens are small mesophylls (notophylls), *c.* 5–6 cm long and *c.* 3–5 cm wide at the widest part (Fig. 2a–d). They are pinnatifid (deeply pinnately lobed), with up to 8–10 alternate to subopposite lobes with a decurrent basal margin and an apical margin that meets the medial part of the leaf at an acute angle. The sinuses between the lobes are acute and have sharp, not rounded, margins. Individual lobes bear 0–4 marginal teeth (1–2 mm long) with slightly flexuous basal flanks and straight to convex apical flanks. Sinuses between the teeth range from acute to right angled with both sharp and rounded margins. As described by Archangelsky (1963), a few specimens are bipinnate fronds with pinnatifid pinnae (Fig. 2b). Archangelsky & Petriella (1971) interpreted the variation among leaf types as developmental stages (presumably meaning variation in leaves along a shoot rather than stages in the development of individual leaves). It is unclear how much of this variation is original, and how much is due to degrees of fragmentation of bipinnate leaves.

The leaves (pinnae) have a thickened primary vein that gives off one secondary vein per lobe. Each secondary vein enters the lobe close to its apical (acroscopic) side and runs to its apex. The remaining laminar venation consists of one order of finer tertiary veins, which irregularly dichotomize and anastomose to form a reticulum of elongated areoles. These veins join at the margin to produce an intramarginal vein. No freely ending veinlets are present. The venation is extremely sparse, with an average vein density (obtained from measurements on three random areas of leaves) of 1.3 mm of vein length mm^{-2}. Venation of the teeth corresponds to the chloranthoid type (Hickey & Wolfe, 1975; Doyle, 2007), with one medial and two lateral veins that fuse to form a tripod. A typical apical gland may be present, but this is not definitively established.

Cuticular micromorphology of Mesodescolea

The cuticle of *Mesodescolea* shows generally isodiametric pavement (unspecialized) cells with straight anticlinal walls (Fig. 3a–c). The stomatiferous cuticle bears irregularly oriented stomata. The guard cells are 26–38 (32.8) μm long and have poles at the same level as the aperture. Each

pair of guard cells has a complex vestibulum with massively thickened outer ledges and thinner inner ledges. The cuticle at each pole of the guard cells has a pronounced T-shaped thickening (T-piece: Fig. 3d–e). The guard cell pairs are more or less circular, with a length to width ratio of *c.* 1.4 (1.2–1.6). The stomatal complexes are most commonly laterocytic, with a significant minority of paracytic and stephanocytic complexes (Fig. 3a–c). Subsidiary cells that are shorter than the guard cells (Fig. 3c) and other irregularities are present. The structures previously described as trichome bases do not show any abscission scars, and there is no indication of a raised basal cell or cuticular intrusions between the basal cell and the surrounding pavement cells (Fig. 3a,f). The cuticle is usually perforated on the central cell of the complex, and the striations from the surrounding cells partially cover the central cell (Fig. 3f).

Cuticle ultrastructure

The cuticle of non-stomatiferous pavement cells in *Mesodescolea* is 5 μm (3.4–7.3) thick. Epicuticular osmiophilic bodies 27 nm (11–49) in size are present. Two layers (A and B, respectively outer and inner) can be identified in the cuticle (Fig. 4a). The A layer (cuticle proper) is 0.75 μm (0.36–1.5) thick. It consists of a thin, laminar A1 layer 0.04 μm (0.008–0.1) thick, which is commonly not preserved, and an A2 layer 0.7 μm (0.3–1.5) thick, which is alveolar-granular with small, irregularly distributed alveoli interconnected with short channels (Fig. 4b,c,d). Some sections show larger alveoli (mean diameter 40 nm) on the inner side of the layer, interconnected by short channels (Fig. 4b,c).

The B layer is 3.7 μm (2.1–6.9) thick, and has anticlinal pegs. It consists of an electron-dense B1 layer 3.5 μm (2–6.7) thick, with an outer granular ($B1_U$) and an inner granular-fibrillar ($B1_L$) zones, and a B2 (granular) layer (Fig. 4b,d,f). The $B1_U$ zone is homogeneous, with sparse small alveoli to the outside (Fig. 4b). The $B1_L$ zone has a compact zone of granules 13 nm (8–23) thick (Fig. 4b,d), grading into fibrillar organization, with some reticulate and pillar-like structures, to the inside (Fig. 4e).

The B2 layer is difficult to distinguish, being a thin, homogeneous granular electro-lucent zone 0.13 μm (0.10–0.18) thick (Fig. 4f).

Phylogenetic analyses

In the MP analysis, with all three backbone trees (Fig. 5; Fig. S1), *Mesodescolea* has three most parsimonious positions, all in Austrobaileyales: sister to *Austrobaileya*, to *Trimenia*, and to

Schisandra. The positions with *Austrobaileya* and *Schisandra* are supported by predominantly laterocytic stomata (character 20), whereas the link with *Trimenia* is supported by the presence of an intramarginal or fimbrial vein (15). Positions elsewhere in Austrobaileyales and on its stem lineage are one step less parsimonious (MP+1). All these positions are supported by T-pieces (22), a synapomorphy of Austrobaileyales (with convergent origins in Atherospermataceae and Buxaceae).

Several other features of *Mesodescolea* place broader constraints on its position. With the D&E and Li *et al.* trees, oil cells (26) are a synapomorphy of Austrobaileyales and mesangiosperms that was lost in eudicots and in monocots other than *Acorus*. With the J/M backbone, it is equivocal whether oil cells originated once, twice, or three times, but because oil cells are lacking in eudicots and most monocots, placing *Mesodescolea* in these clades adds a step. Oil cells reappear in some derived core eudicots, but in basal eudicots they are known only in the stems of some Menispermaceae and Proteaceae, and not the leaves (Baas & Gregory, 1985). With the D&E and Li *et al.* trees, the Zone I pattern of stomatal variation (21) is ancestral in angiosperms but is lost in the common ancestor of eudicots, monocots, and magnoliids, which tends to restrict *Mesodescolea* to the ANITA lines and Chloranthaceae; with the J/M tree, the number of losses is equivocal. Similarly, with the D&E tree, chloranthoid teeth (19) are ancestral in angiosperms and were lost on the line leading to monocots and magnoliids, which tends to exclude *Mesodescolea* from these clades. The history of this character is equivocal with the J/M and Li *et al.* trees, but again it favors positions outside magnoliids and monocots.

With all three backbone trees, *Mesodescolea* has four MP+1 positions in Chloranthaceae: sister to *Ascarina*, to *Sarcandra*, to *Chloranthus*, and to the *Sarcandra–Chloranthus* clade. The positions with *Sarcandra* and *Chloranthus* are supported by predominantly laterocytic stomata (modified to predominantly paracytic in *Chloranthus*), whereas the link with *Ascarina* is supported by elongate tertiary vein areas (12). These positions are consistent with the presence in Chloranthaceae of epidermal oil cells (27; *Ascarina*, *Sarcandra*) and Zone I stomatal variation (*Sarcandra*, *Chloranthus*; inapplicable in *Hedyosmum* and *Ascarina*, which have stephanocytic stomata).

With the D&E backbone (Fig. 5), another MP+1 position of *Mesodescolea* is sister to *Ceratophyllum*, a submerged aquatic with dichotomous leaves and no stomata. This result is supported only by leaf dissection (18); it appears to be an artifact caused by the high number of

inapplicable characters in *Ceratophyllum* and its sister-group relationship to Chloranthaceae, which share features with *Mesodescolea*. It is less parsimonious (MP+2) with the J/M and Li *et al.* trees, in which *Ceratophyllum* is sister to eudicots.

Positions on the internal branches between the stem node of Nymphaeales and the mesangiosperm node are two steps less parsimonious than the best positions. Positions in eudicots are at least three steps less parsimonious with the D&E tree, four with the J/M and Li *et al.* trees, partly because of the absence of oil cells in eudicots and the prevalence of anomocytic stomata in Ranunculales. Its least unparsimonious positions are sister to Papaveraceae and to *Circaeaster*, which also lack freely ending veinlets (14), and to Menispermaceae, which have a fimbrial vein.

In its most parsimonious positions, *Mesodescolea* has several autapomorphies that reflect major morphological divergence from its closest relatives. These are leaf dissection (18), absence of freely ending veinlets (14, also seen in Nymphaeales and a few mesangiosperm taxa), and one order of reticulate venation (11), plus elongate tertiary areas (12) and intramarginal vein (15), except when *Mesodescolea* is linked with *Trimenia*, which has an intramarginal vein and was scored as uncertain (0/1) for tertiary areas. Most of these features are also autapomorphies of *Mesodescolea* when it is nested in Chloranthaceae.

The MP bootstrap analysis (Fig. 6a, Fig. S2a,c) shows that the best-supported position for *Mesodescolea* on all three backbones is in a clade with Austrobaileyales, with a bootstrap value (summing values for all positions in the clade and on its stem lineage) of 60% on the D&E backbone, 64% on the J/M backbone, and 63% on the Li *et al.* backbone. Dissecting the signal using RoguePlot, the best-supported placement is sister to *Trimenia* (found in 26%, 31%, and 31% of the bootstrap trees with the D&E, J/M, and Li *et al.* backbones, respectively), followed by placement sister to *Austrobaileya* (21%, 21%, and 20%). A position sister to either *Ceratophyllum* or *Ascarina* is retrieved in around 10% of the replicates on all three topologies (15%, 11%, and 10% for *Ceratophyllum*; 10%, 10%, and 12% for *Ascarina*). Placements sister to Papaveraceae, Menispermaceae, *Sarcandra* plus *Chloranthus*, and at other positions in the Austrobaileyales and Nymphaeales are retrieved at much lower frequencies on all or some of the backbone topologies.

BI (Fig. 6b, Fig. S2b,d) shows similar support for a placement of *Mesodescolea* in a clade with Austrobaileyales (posterior probability of 0.86, 0.88, and 0.90). The best placement on all tree topologies is sister to *Illicium* plus *Schisandra* (0.22, 0.23, and 0.22), but positions sister to *Trimenia* (0.16, 0.21, and 0.17) and *Schisandra* (0.14, 0.19 and 0.18) are almost as probable. A

placement sister to *Austrobaileya* is almost equally probable on the D&E and Li *et al.* backbones, but not on the J/M backbone (0.16, 0.08, and 0.18). Most other placements receive negligible support.

Phylogenetic hypothesis testing

Support strength as measured by Bayes factors is described as very strong (2lnBF >10), strong (2lnBF 6–10), positive (2lnBF 2–6), or not worth a bare mention (2lnBF 0–2), following Kass & Raftery (1995). The Bayes factor analysis (Table 1) shows positive support for the placement sister to Austrobaileyales over other placements, with the strength of support varying across the three backbone topologies. Using the D&E backbone, a position sister to *Ceratophyllum* is almost as good as one sister to Austrobaileyales (2lnBF = 0.7), but this position is worse on the Li *et al.* and J/M backbones (2lnBF = 4.7 and 4.96, respectively). This is consistent with the lower parsimony of the *Mesodescolea–Ceratophyllum* link on the J/M and Li *et al.* backbone trees. The position sister to Austrobaileyales has strong support over positions sister to mesangiosperms and to the clade of Austrobaileyales plus mesangiosperms on the D&E backbone (2lnBF = 6.1 and 6.18, respectively), whereas it has weaker but still positive support on the Li *et al.* backbone (2lnBF = 5.72 and 4.9), and stronger support on the J/M topology (2lnBF = 8.62 and 10.1). A placement sister to Chloranthaceae is worse than one sister to Austrobaileyales on all three backbones (4.6 on the D&E backbone, 5.52 on the J/M backbone, and 4.46 on the Li *et al.* backbone). The placement sister to Austrobaileyales is also very strongly supported over placements sister to eudicots and to Ranunculales on all backbone topologies (2lnBF = 11.1, 10.66, and 10 for eudicots and 14.88, 13.96, and 15.24 for Ranunculales). Evidence against a position sister to Papaveraceae is very strong on the D&E topology (2lnBF = 10.34) and strong on the other two topologies (9.92 and 9.7 on the J/M and Li *et al.* backbones, respectively).

Discussion

Our results indicate that the similarities between *Mesodescolea* and *Stangeria* are superficial. Cuticular striations, which in cycads are unique to *Stangeria* and a few unrelated extinct taxa (*Ctenis, Pterostoma*), are widespread among angiosperms (Rao, 1939; Behnke & Barthlott, 1983). The structures previously identified as trichome bases (Archangelsky, 1963; Archangelsky & Petriella, 1971; Artabe & Archangelsky, 1992) lack the basal cell with a rounded section,

abscission scar, and funnel-shaped cuticular plug found in *Stangeria* (Fig. S3c). Instead, they show cuticular striations that partially cover the central cell, commonly with an irregular central perforation, as is typical of glandular structures. Most strikingly, *Mesodescolea* has angiosperm-like guard cells with poles at the level of the aperture, whereas *Stangeria* has typical gymnospermous guard cells (Fig. S3), with poles bent up above the aperture (Porsch, 1905; Harris, 1932). The cuticle ultrastructure of *Mesodescolea*, with a thin A1, granular A2, and granular-fibrillar B layer, differs from that typical of cycads, with a thick and lamellated A1, amorphous A2, and channeled B layer with pectin intrusions (Villar de Seoane, 1997; Bajpai, 2000; Barone Lumaga *et al.*, 2015). The fine veins of *Mesodescolea* anastomose irregularly, with the outermost anastomoses forming an intramarginal vein, but *Stangeria* has parallel veins that diverge regularly from the leaflet midrib and end at the margin (Erdei & Manchester, 2015). The leaf architectural variation that Archangelsky & Petriella (1971) interpreted in ontogenetic terms also contrasts with the typical development of cycad leaves (Johnson, 1943; Stevenson, 1981).

Mesodescolea *and other fossil gymnosperms*

Reticulate fine venation, stomatal poles level with the aperture, and stomatal ledges forming a vestibulum separate *Mesodescolea* from most gymnospermous leaves. An exception is *Sagenopteris* (Caytoniales), which also has fine veins forming a reticulum of elongate areoles, stomatal poles level with the aperture, and stomatal ledges (Harris, 1940; Barbacka & Bóka, 2000; Elgorriaga *et al.*, 2019). However, *Sagenopteris* is palmately compound, with leaflets in which the midrib is 'consumed' by divergence of lateral veins before reaching the apex, whereas *Mesodescolea* is pinnately lobed and has craspedodromous secondaries. Moreover, although *Sagenopteris* has trichomes, it lacks the radiostriate idioblasts typical of *Mesodescolea.* *Petriellaea*, which has cupules reminiscent of Caytoniales (Taylor *et al.*, 1994) but palmately dissected leaves (*Rochipteris*), also has one order of laminar venation forming elongate areoles (Bomfleur *et al.*, 2014).

Simple reticulate venation with elongate areoles also occurs in glossopterids, *Ctenis*, and other fossil taxa (Trivett & Pigg, 1996), but without the angiosperm-like epidermal features of *Sagenopteris*. *Ruflorinia*, also from the Baqueró Group (Archangelsky, 1963), has bipinnate leaves superficially similar to *Mesodescolea* but open fine venation and sunken stomata surrounded by papillate subsidiary cells. Judging from the illustrations of Villar de Seoane (2000) and Carrizo *et al.* (2014), *Ruflorinia* may have guard cell poles level with the aperture and outer stomatal ledges,

as in angiosperms and *Sagenopteris*, consistent with the associated *Caytonia*-like cupulate structures (*Ktalenia*: Taylor & Archangelsky, 1985). In Gnetales, *Welwitschia*, *Gnetum*, and several Cretaceous fossils have reticulate venation and paracytic stomata. *Cearania*, with paracytic stomata but parallel venation, has somewhat different striate idioblasts (Kunzmann *et al.*, 2009). However, reticulate venation in Gnetales exhibits a "chevron" pattern (*Welwitschia*, *Drewria*) or several angiosperm-like vein orders (*Gnetum*), and pinnate dissection, chloranthoid teeth, stomatal ledges, and T-pieces are unknown.

Angiosperm affinities of Mesodescolea

The stomatal features just cited and chloranthoid teeth together support an angiosperm affinity for *Mesodescolea*. In addition, it shares special similarities with angiosperm leaves and dispersed angiosperm cuticles from the lower Potomac Group (Upchurch, 1984b), or palynological Zone I of Brenner (1963), dated as Aptian to earliest Albian (Doyle & Endress, 2014; Doyle & Upchurch, 2014; Tanrikulu *et al.*, 2018). One is the unusual variability in number and arrangement of subsidiary cells, with stomata varying between paracytic, laterocytic, and stephanocytic and showing such irregularities as subsidiaries that do not extend the full length of the guard cells. Upchurch (1984a) and Carpenter (2005, 2006) recognized similar variation in *Amborella*, *Austrobaileya*, *Schisandra*, and Chloranthaceae. Other 'Zone I' features of *Mesodescolea* are T-pieces at the stomatal poles and radiostriate idioblasts, which appear to be intrusive epidermal oil cells. Oil cells are characteristic of Austrobaileyales, Chloranthaceae, and magnoliids, where they occur consistently in the mesophyll and commonly in the epidermis as well. However, the Zone I leaves differ in being unlobed and pinnately veined and having more orders of reticulate venation.

Our analyses confirm the phylogenetic significance of these Zone I features. The best-supported positions of *Mesodescolea* are in Austrobaileyales, the third line in the ANITA grade, but there is some weaker evidence for a relationship to Chloranthaceae. These positions are supported by chloranthoid teeth, predominantly laterocytic stomata, Zone I stomatal variation, T-pieces, and oil cells. However, our tests of phylogenetic uncertainty suggest it may be premature to reject the possibility that *Mesodescolea* represents an additional extinct line in the ANITA grade. There is distinctly less support for a position in eudicots, despite the dissected leaves and chloranthoid teeth of many Ranunculales.

Mesodescolea diverges markedly from its inferred extant relatives in leaf dissection, one order

of reticulate venation, elongate areoles, and lack of freely ending veinlets. An intriguing possibility is that these are not autapomorphies but rather 'gymnospermous' states that reflect a position on the angiosperm stem lineage. Our analyses did not include outgroups, since there is no consensus on fossil relatives of the angiosperms (Doyle, 2012). Hence character polarity is inferred from the molecular rooting and internal topology of the angiosperms. A stem position for *Mesodescolea* adds three steps, since it has laterocytic stomata, oil cells, and T-pieces, which are absent in *Amborella* and Nymphaeales. However, two proposed angiosperm outgroups, *Caytonia* and *Petriellaea* (Doyle, 2008; Bomfleur *et al.*, 2014; Coiro *et al.*, 2018), have compound and dissected leaves with simple reticulate venation, elongate areoles, and no freely ending veinlets. If such fossils are related to angiosperms, these characters would increase support for placement of *Mesodescolea* on the angiosperm stem lineage.

Potentially related Cretaceous leaves

Several Early Cretaceous lobate leaf types merit discussion as possible relatives of *Mesodescolea*. Some have been compared with Ranunculales, which often have ternately dissected leaves (Vakhrameev & Krassilov, 1979; Doyle, 2001, 2007; Krassilov & Volynets, 2008). This poses a problem, since Ranunculales, like other basal eudicots, have tricolpate and derived pollen types, but some of the leaves predate the first reports of tricolpates in their respective areas (Fig. 7). *Mesodescolea* exemplifies this situation: the Baqueró palynoflora contains diverse angiospermous monosulcates (Archangelsky & Archangelsky, 2013; Llorens & Perez Loinaze, 2016), but no tricolpates, which are generally not reported in Argentina before the early Albian (Archangelsky *et al.*, 2009; for a possible exception, see Guler *et al.*, 2015). Similar cases are ternate leaves from the Aptian of central Argentina (Puebla, 2009), and pinnately lobed leaves with one order of fine venation (*Iterophyllum*) from the Barremian of Spain (Barral *et al.*, 2013). Mohr & Friis (2000, fig. 2G) illustrated a late Aptian lobed leaf from the Crato Formation of Brazil, but in this case tricolpate pollen does occur in the same formation (Heimhofer & Hochuli, 2010).

The Potomac genus *Vitiphyllum* (Fontaine, 1889; Fig. 8a,b) is a ternately lobed leaf from upper Zone I (earliest Albian), where tricolpates appear (Hickey & Doyle, 1977). A sign that *Vitiphyllum* may not be a eudicot is the presence of dots that resemble oil cells (Fig. 8b). *Potomacapnos* (Jud & Hickey, 2013) is a lobate leaf with elongate areoles, an intramarginal vein, and chloranthoid teeth from lower Zone I (Aptian) at Dutch Gap, where no tricolpates have been found (Upchurch

& Doyle, 1981). Jud & Hickey (2013) assigned *Potomacapnos* to Papaveraceae, but unlike its proposed relatives and like *Mesodescolea* it has only one order of reticulate venation. Fontaine (1889) described *Fairlingtonia* as a fern leaf, but Jud (2015) showed it is a stem bearing ternate leaves (Fig. 8c illustrates a probable Dutch Gap specimen). Vakhrameev (1952) and Vakhrameev & Krassilov (1979) described shoots with *Vitiphyllum*-like leaves and inflorescences (*Caspiocarpus*) from the Albian of Kazakhstan.

Potentially related leaves occur in NE China and the Russian Primorye. In China, these include the latest Barremian aquatic *Archaefructus* (Sun *et al.*, 2002), with finely dissected ternate leaves, and the bizarre leaf genus *Jixia* (Sun & Dilcher, 2002), which is pinnately lobed with reflexed basal lobes. Golovneva *et al.* (2018) reported *Jixia* and fruits called *Achaenocarpites* (Krassilov & Volynets, 2008), associated with shoots bearing ternate leaves recalling *Fairlingtonia*, from the Frentsevka Formation in the Primorye. They concluded that this flora is early or middle Albian, and they argued that the Chinese flora containing *Jixia* is the same age (rather than Hauterivian or Barremian: Sun & Dilcher, 2002). Tricolpates occur in the Frentsevka Formation (Markevich, 1995). Krassilov (1967) described *Sujfunophyllum* from the correlative Galenkov Formation as a palmately dissected gymnosperm leaf with a bifurcating lamina. However, in its leaf form, occasional vein anastomoses, and intramarginal vein, *Sujfunophyllum* is similar to *Mesodescolea*.

Another potentially relevant taxon is *Eucalyptophyllum*, one of the Potomac leaves in which Upchurch (1984a,b) recognized the Zone I cuticle syndrome. It is like leaves of Austrobaileyales in being simple and pinnately veined, but like *Mesodescolea* in having an intramarginal vein, elongate tertiary areas, and no freely ending veinlets. *Kachaikenia*, from the Albian of Argentina (Cunéo & Gandolfo, 2005), also has elongate areoles and an intramarginal vein, but it is like *Mesodescolea* in being pinnately lobed, and like *Eucalyptophyllum* in lacking teeth.

Cuticle studies are clearly desirable in order to test relationships of Early Cretaceous lobate leaves with *Mesodescolea*. Associated fruits could also be informative. Some in the Primorye are described as follicles (e.g., *Ternaricarpites*: Krassilov & Volynets, 2008; Golovneva *et al.*, 2018), but we see no evidence that they actually dehisced. Most living members of the ANITA grade have indehiscent fruits, except *Illicium*.

Ecophysiological implications

If *Mesodescolea* is in the ANITA grade, its single order of reticulate venation and lack of freely ending veinlets represent reversals of two angiosperm synapomorphies. It would also have undergone a reduction in vein density, which is 1.3 mm mm^{-2} in *Mesodescolea*, comparable to gymnospermous groups such as Caytoniales, Ginkgoales, and cycads and many ferns (Boyce *et al.*, 2009), but is 1.94–6.35 mm mm^{-2} in *Amborella* and Austrobaileyales and has been reconstructed as 3.36 mm mm^{-2} in the common ancestor of angiosperms (Feild *et al.*, 2011). By contrast, if *Mesodescolea* is an angiosperm stem relative, its low vein density may be ancestral.

Since increased vein density is related to increased gas exchange potential (Boyce *et al.*, 2009; Feild *et al.*, 2011), the low vein density in *Mesodescolea* suggests it was under low pressure for gas exchange. Argentina was located in the wet temperate Southern Gondwana province (Brenner, 1976), where a decrease in vein density might be tolerated. In its low vein density and high degree of lobation, *Mesodescolea* resembles many ferns. If it was competing primarily with ferns, it may have had a competitive advantage due to its lack of a slow-growing and vulnerable gametophyte phase.

Considering other features of *Mesodescolea*, lobation is associated with carbon-acquisitive, water-wasting leaves in *Pelargonium* (Nicotra *et al.*, 2008). This would be consistent with a fast-growing, opportunistic growth strategy, as proposed for the Russian lobate leaves (Krassilov & Volynets, 2008; Golovneva *et al.*, 2018). If the teeth were hydathodal, as in Chloranthaceae, they might prevent flooding of the mesophyll during periods of high humidity and/or fast growth (Feild *et al.*, 2005; Barral *et al.*, 2013). Some cuticular features seen in *Mesodescolea* (large vestibulum, cuticular striations) have been associated with wet understory conditions, e.g. in Proteaceae (Feild & Arens, 2005) and *Austrobaileya* (Feild *et al.*, 2003). In its cuticle ultrastructure, the absence of lucent amorphous material and the presence of well-developed fibrils and pillar-like structures suggest adaptation to shade (Guignard *et al.*, 2001).

The diverse plant assemblage associated with *Mesodescolea* indicates a humid warm-temperate climate, with occasional stress caused by volcanic activity (Archangelsky *et al.*, 1995). Its taxonomic composition suggests a well-developed multistratal forest, with emergent and canopy layers of conifers and Ginkgoales, an understory shrub layer of Cycadales, ‘seed ferns’, and Bennettitales, and a herbaceous layer of ferns and angiosperms (Archangelsky, 1963, 1966; Archangelsky & Petriella, 1971; Romero & Archangelsky, 1986; Passalía *et al.*, 2003; Del Fueyo *et al.*, 2007; Romero *et al.*, 2016; Coiro & Pott, 2017). These data are consistent with evidence

from leaf characters that *Mesodescolea* grew in the wet forest understory, the sort of habitat reconstructed by Feild *et al.* (2004) as ancestral in angiosperms.

Conclusions

Based on this study, *Mesodescolea* reveals the existence of highly unexpected morphological trends within one of the surviving low-diversity lines in the early angiosperm radiation, the Austrobaileyales, or else it represents a previously unsuspected extinct line. Depending on how many other Cretaceous leaves are related to *Mesodescolea*, this lineage may have made up a sizeable proportion of the Aptian-Albian angiosperm flora.

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Data availability

The Nexus file used for our phylogenetic analysis and the trees used to generate the RoguePlots are available on FigShare: 10.6084/m9.figshare.11841588

Author contributions

MC designed the research, with inputs from JAD and GRU. MC, LCAM, JAD, and GRU collected data. MC and JAD analyzed data. MC, JAD, and LCAM drafted the figures. MC and JAD wrote the manuscript with significant inputs from GRU and LCAM. All authors read and approved the final version of the manuscript.

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Supporting information captions

Methods S1: Methods for the preparation and observation of cuticles of extant *Stangeria eriopus.*

Notes S1: Characters and taxa used in our phylogenetic analyses, with description and justification of the characters.

Table S1: Fossil specimens observed in this study.

Fig. S1 Results of parsimony analysis of positions of *Mesodescolea* on the Li *et al*. and J/M backbone trees of living angiosperms.

Fig. S2 RoguePlots showing the support for the placement of *Mesodescolea* on the Li *et al*. and J/M backbone trees of living angiosperms.

Fig. S3 Cuticular morphology of *Stangeria eriopus*.

Figure legends

Fig. 1 Geographic and geological setting of the Baqueró Group and the Anfiteatro de Ticó formations (redrawn from Cladera *et al.,* 2002), and geochronological age for the Baqueró Group.

Fig. 2 Macromorphology of *Mesodescolea.* (a) Leaves with lobes showing differing degrees of dentation, as well as differentiation of the primary (black arrowhead) and secondary veins (white arrowheads). (b) Leaves showing bipinnate organization. (c) General morphology of leaves, showing some details of the venation. (d) Detail of (c), showing the irregularly anastomosing venation and the intramarginal vein. (a) Specimen LPPB 5126, (b) specimen LPPB 5387, (c,d) specimen LPPB 4966. Bars = 1 cm.

Fig. 3 Cuticular micromorphology of *Mesodescolea*. (a) Light micrograph of the stomatiferous cuticle. White arrowheads indicate radiostriate idioblasts (intrusive oil cells). (b, c) CLSM optical sections at different focal depths, showing the outer cuticle (b) and the inner cuticle (c) surfaces. (d) Detail of (c). T-pieces are indicated by black arrowheads. (e) Light microscopic detail of

stomata. Black arrowheads indicate T-pieces. (f) CLSM maximum intensity projection of a radiostriate idioblast, showing the radiating shapes of the surrounding cells, cuticular striations, and perforated cuticle of the central cell. Bars (a,e) = 100 µm, (b,c,d,f) = 50 µm. Abbreviations: lat = laterocytic, par = paracytic, ste = stephanocytic. (a) Specimen v51294; (b,c,d,f) specimen v44684; (e) specimen v51293.

Fig. 4 *Mesodescolea plicata.* TEM of epidermal cuticle . (a, b) General view of non-stomatiferous pavement cell cuticle, epicuticular components (white arrows) and anticlinal walls (AW), with cuticle proper (A) and cuticular layer (B): A1 (laminar), A2 (alveolar-granular), $B1_U$ (granular) and $B1_L$ (granular-fibrillar) layers. (c) Detail of A1, A2 and $B1_U$ layers, with epicuticular components (white arrows) and large alveoli (black arrows). (d) A1, A2, $B1_U$ and $B1_L$ layers, with epicuticular components (grey arrows), pillar-shape structures (black arrows) and reticulum (white arrows). (e) Detail of $B1_U$ and $B1_L$ zones, with fribrils and granules (white arrows). (f) Detail of $B1_L$ zone with fibrils, granules and reticulum (white arrows), B2 layer (granular) and remains of cell walls (W). Bars = 1 µm. (a-f) Specimen BA Pb MET 103.

Fig. 5 Results of parsimony analysis of positions of *Mesodescolea* on the D&E backbone tree of living angiosperms (Endress & Doyle, 2009). Colors of branches indicate most parsimonious (MP) positions and positions that are one (MP+1), two (MP+2), and three (MP+3) steps less parsimonious. Synapomorphies supporting most parsimonious positions of *Mesodescolea* are indicated with blue arrows (imv = intramarginal vein). Abbreviations: Nymphae = Nymphaeales, Austro = Austrobaileyales, Chlor = Chloranthaceae, Piper = Piperales, Can = Canellales.

Fig. 6 RoguePlots showing support for the placement of *Mesodescolea* using (a) Maximum Parsimony bootstrap, and (b) Bayesian posterior probability. The different colors indicate the percentage of trees with *Mesodescolea* attached to each particular branch. Results are shown for the D&E backbone topology (Endress & Doyle, 2009).

Fig. 7 Sketches of lobate angiosperm leaf types discussed in the text in their stratigraphic and geographic context. Pollen sketches indicate the early Albian appearance of tricolpate eudicot pollen in the sequences considered and the earlier presence of monosulcate angiosperm pollen only. Fossils shown and sources of illustrations used as a basis for sketches: (a) reticulate tricolpate pollen; (b) monosulcate angiosperm pollen; (c) *Mesodescolea* (this article); (d) leaflet of LC-Microphyll trifoliate (Puebla, 2009); (e) *Vitiphyllum* (Berry, 1911); (f) *Fairlingtonia* (Jud,

2015); (g) *Potomacapnos* (Jud & Hickey, 2013); (h) *Iterophyllum* (Barral *et al.*, 2013); (i), *Sujfunophyllum* (Krassilov, 1967); (j) *Achaenocarpites* (Golovneva *et al.*, 2018); (k) *Jixia* (Golovneva *et al.*, 2018); (l) *Archaefructus* (Sun *et al.*, 2002). Sketches of larger leaves (c, e, h, i, k) *c.* 60% actual size; those of smaller leaves (d, f, g, j, l) *c.* 120% actual size.

Fig. 8 *Vitiphyllum multifidum* Fontaine and cf. *Fairlingtonia thyrsopteroides* (Fontaine) Jud. (a) *V. multifidum*, overview of leaf (USNM specimen 31824, Baltimore); (b) detail of the same leaf, showing possible oil cells (arrowheads). (c) Cf. *F. thyrsopteroides,* leaf-bearing shoot (USNM specimen 455017, Dutch Gap; figured by Doyle & Upchurch, 2014, fig. 6c, as 'Leaf-bearing shoot with similarities to *Vitiphyllum parvifolium*'). Bars (a) 1 cm; (b)1 mm; (c) 2 cm.

Table 1: Results of the Bayesian topology testing analysis.

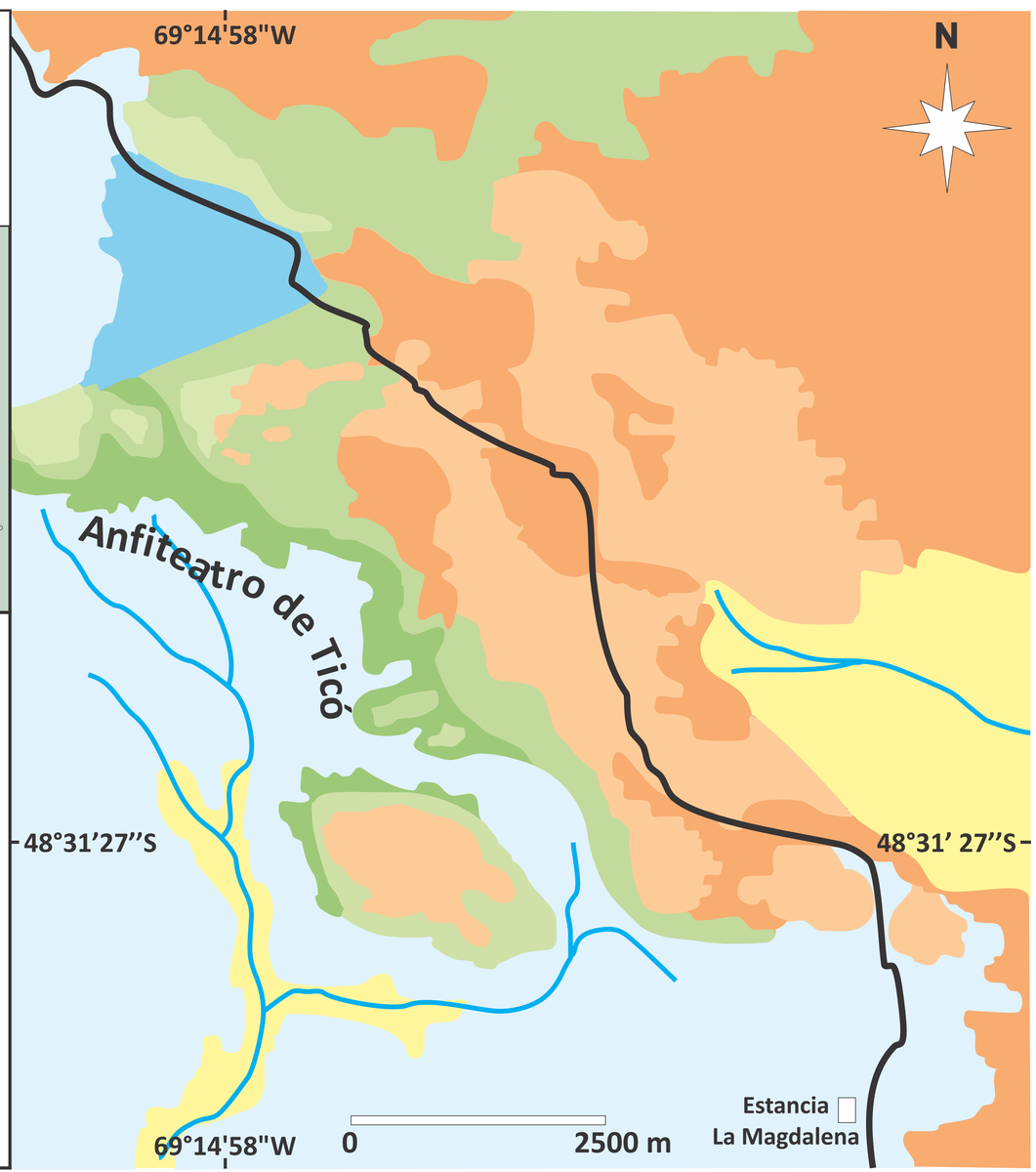
	D&E Marginal Likelihood	Li et al. Marginal Likelihood	J/M Marginal Likelihood	D&E 2lnBF	Li et al. 2lnBF	J/M 2lnBF
Sister to Austrobaileyales	-687.79	-689.19	-690.28			
Sister to Chloranthaceae	-690.09	-691.42	-693.04	4.6	4.46	5.52
Sister to Ranunculales	-695.23	-696.81	-697.26	14.88	15.24	13.96

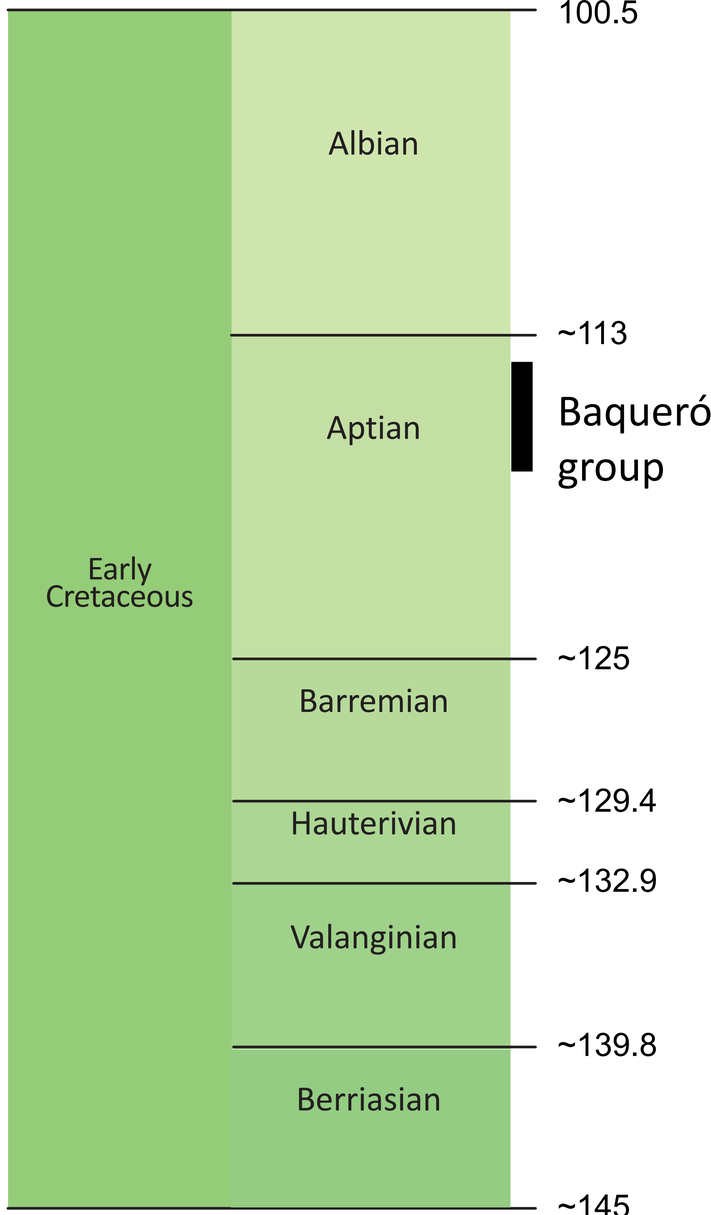
Sister to mesangiosperms	-690.84	-692.05	-694.59	6.1	5.72	8.62
Sister to Papaveraceae	-692.96	-694.04	-695.24	10.34	9.7	9.92
Sister to eudicots	-693.34	-694.19	-695.61	11.1	10.66	10
Sister to Austro + mesang	-690.88	-691.64	-695.33	6.18	3.4.9	10.1
Sister to *Ceratophyllum*	-688.14	-691.67	-692.63	0.7	4.7	4.96

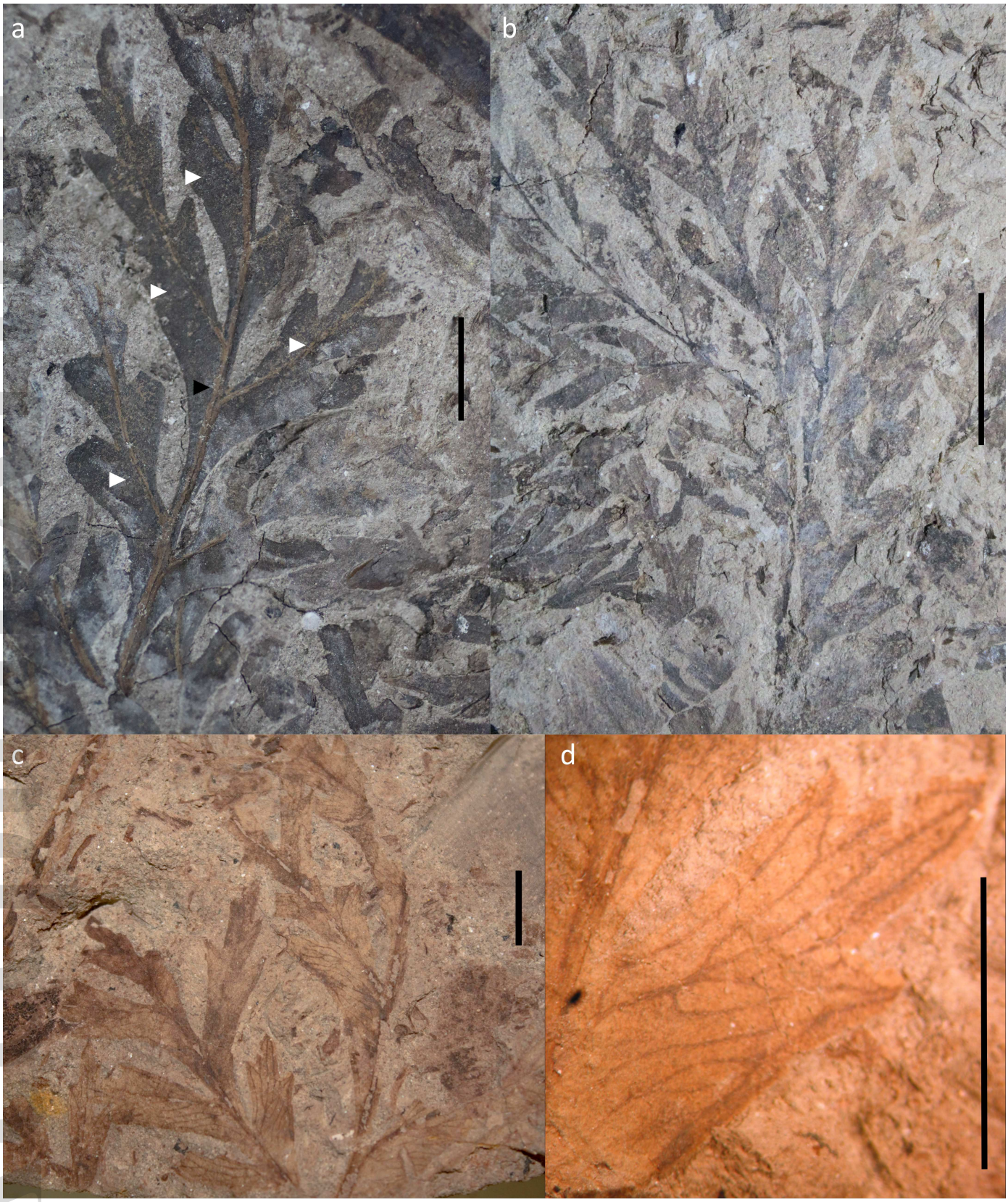
D&E indicates the Endress & Doyle (2009) backbone, J/M indicates the Jansen *et al.* (2007) and Moore *et al.* (2007) backbone, Li et al. indicates the Li *et al.* (2019) backbone.

Formations

- Alluvial deposits/Quaternary
- Monte de León (Oligocene)
- Del Doce (Paleocene-Eocene)
- Baqueró Group
  - Punta del Barco
  - Bajo Tigre
  - Anfiteatro de Ticó
- Bajo Grande (Kimmeridgian-Hauterivian)
- Chon Aike (Bathonian-Callovian)







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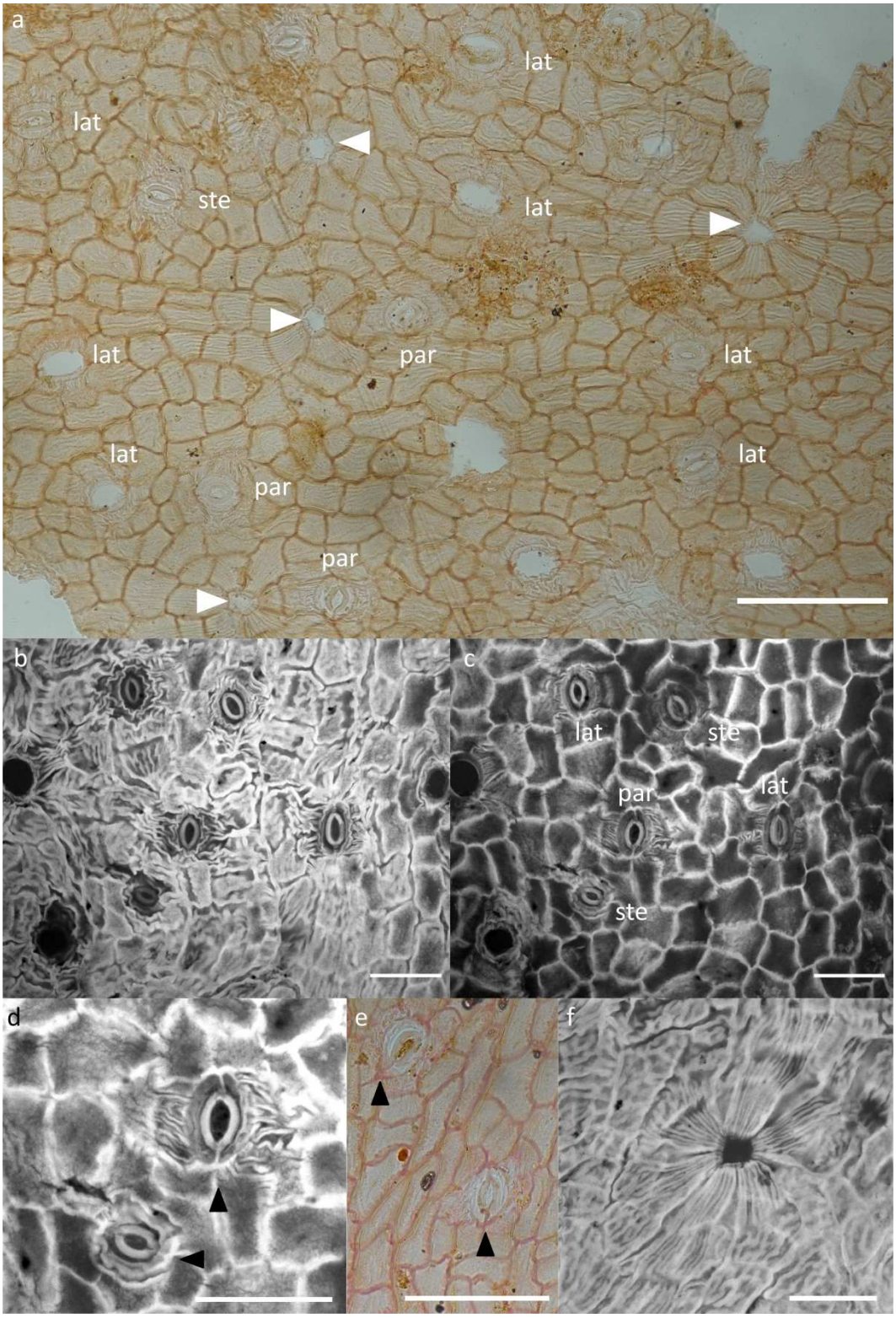

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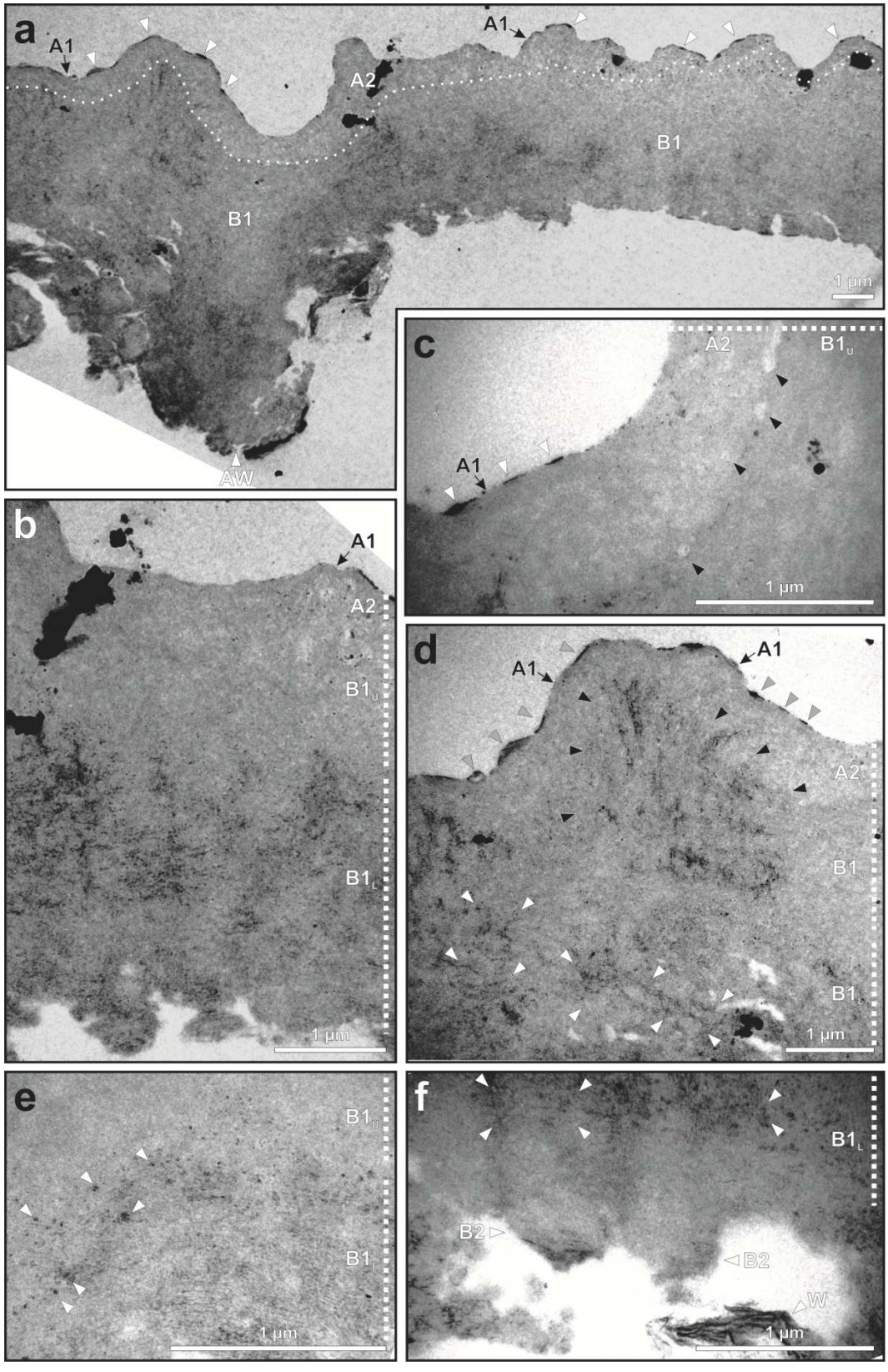

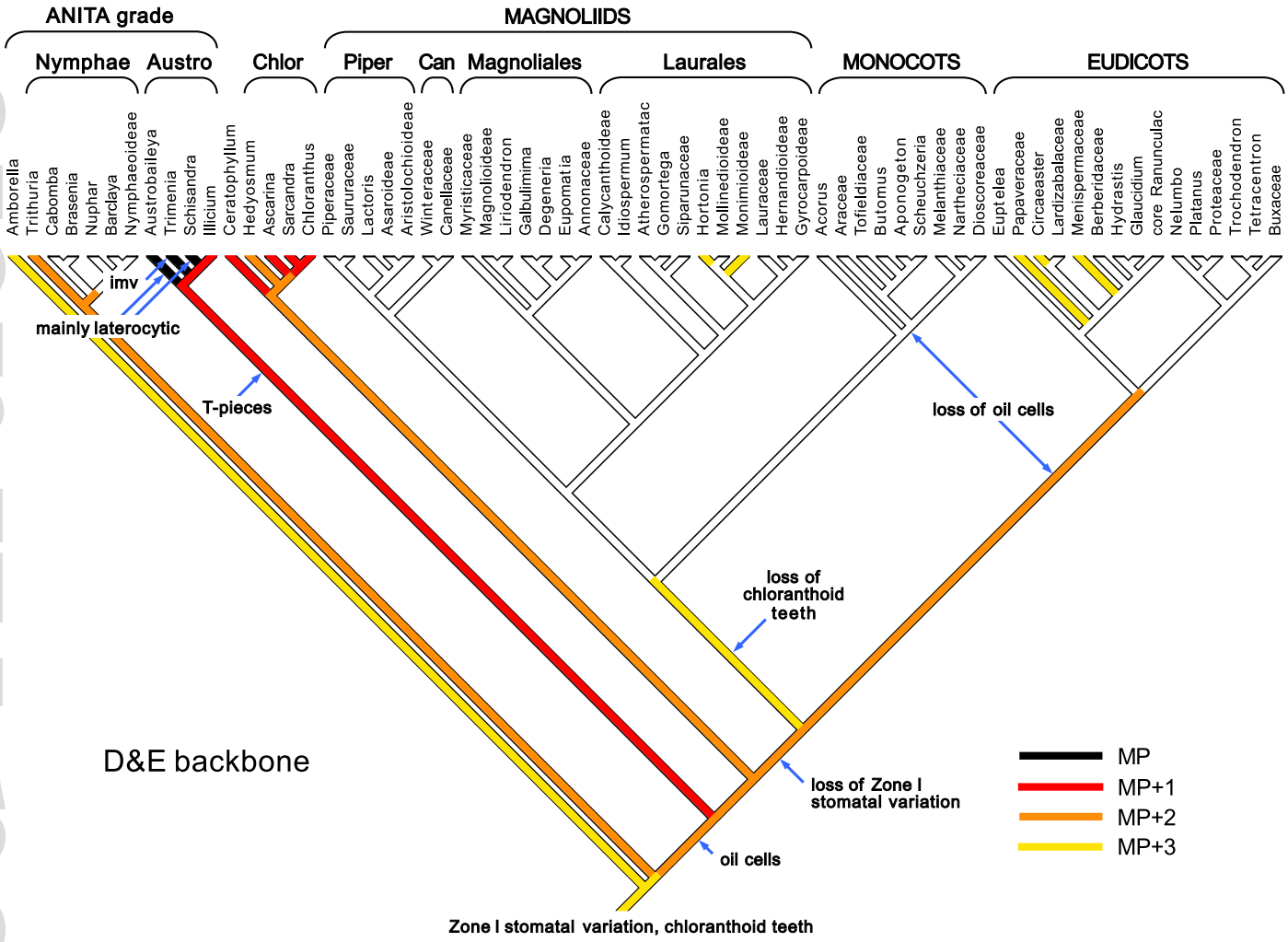

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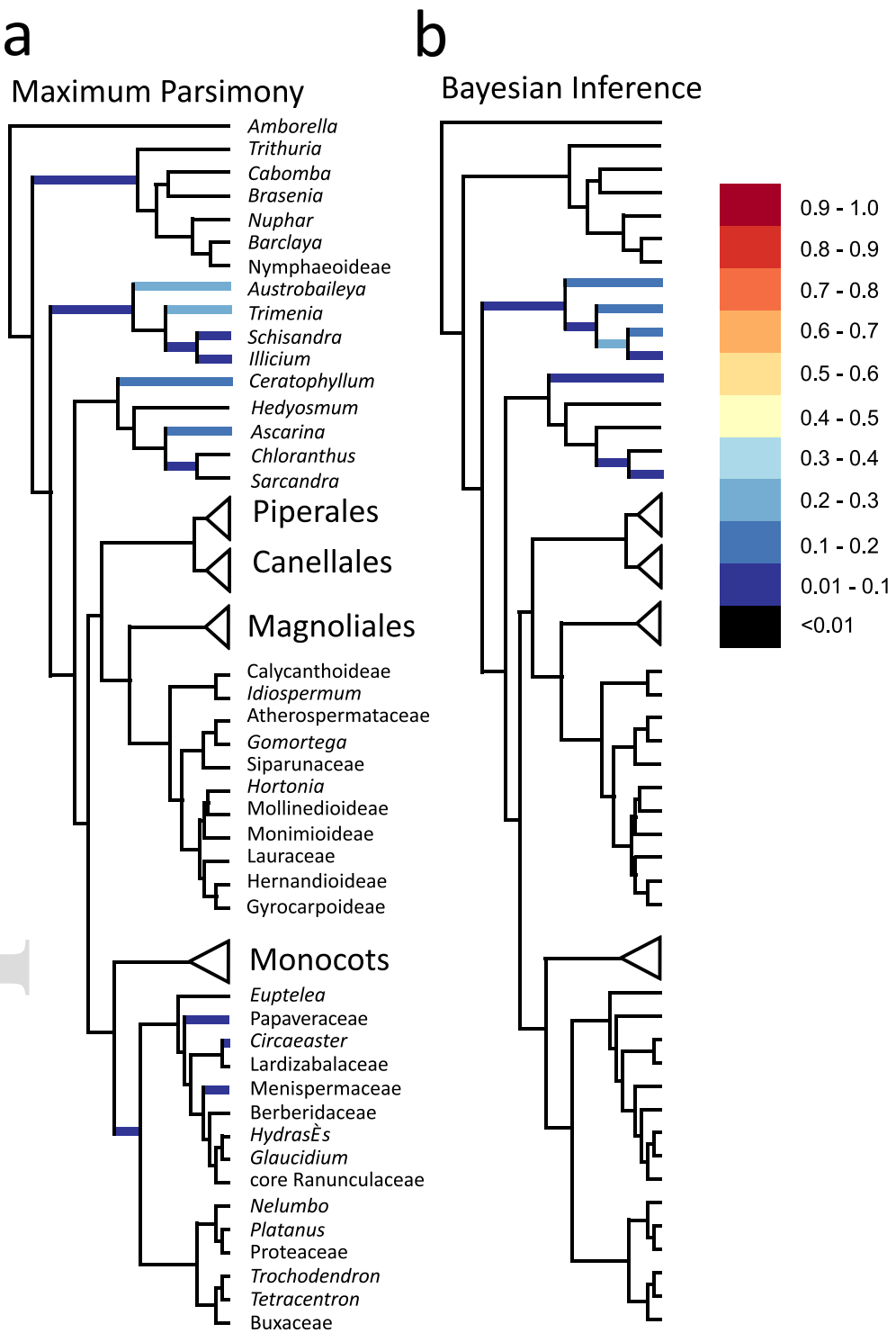

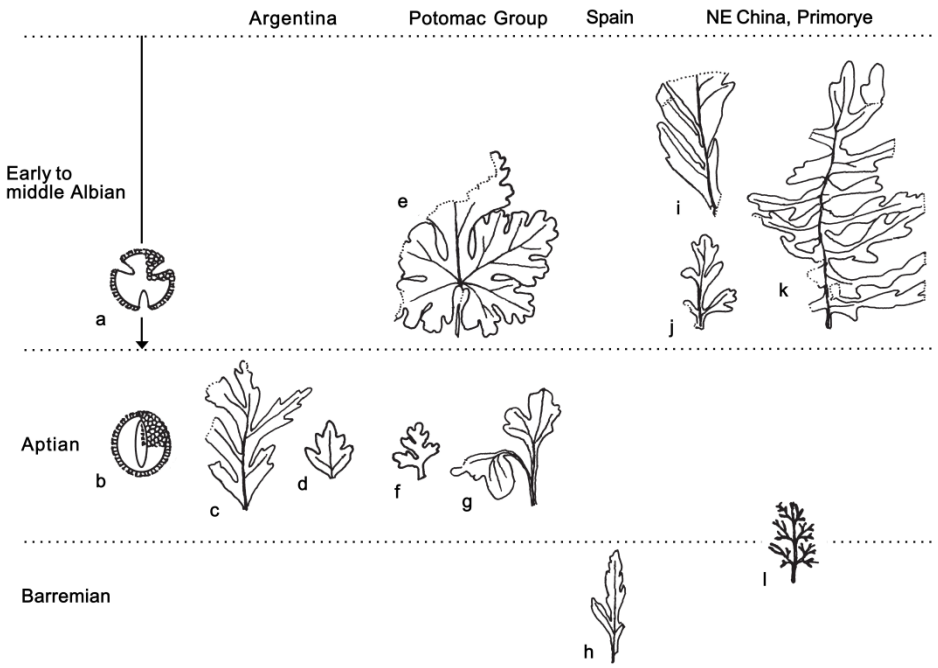

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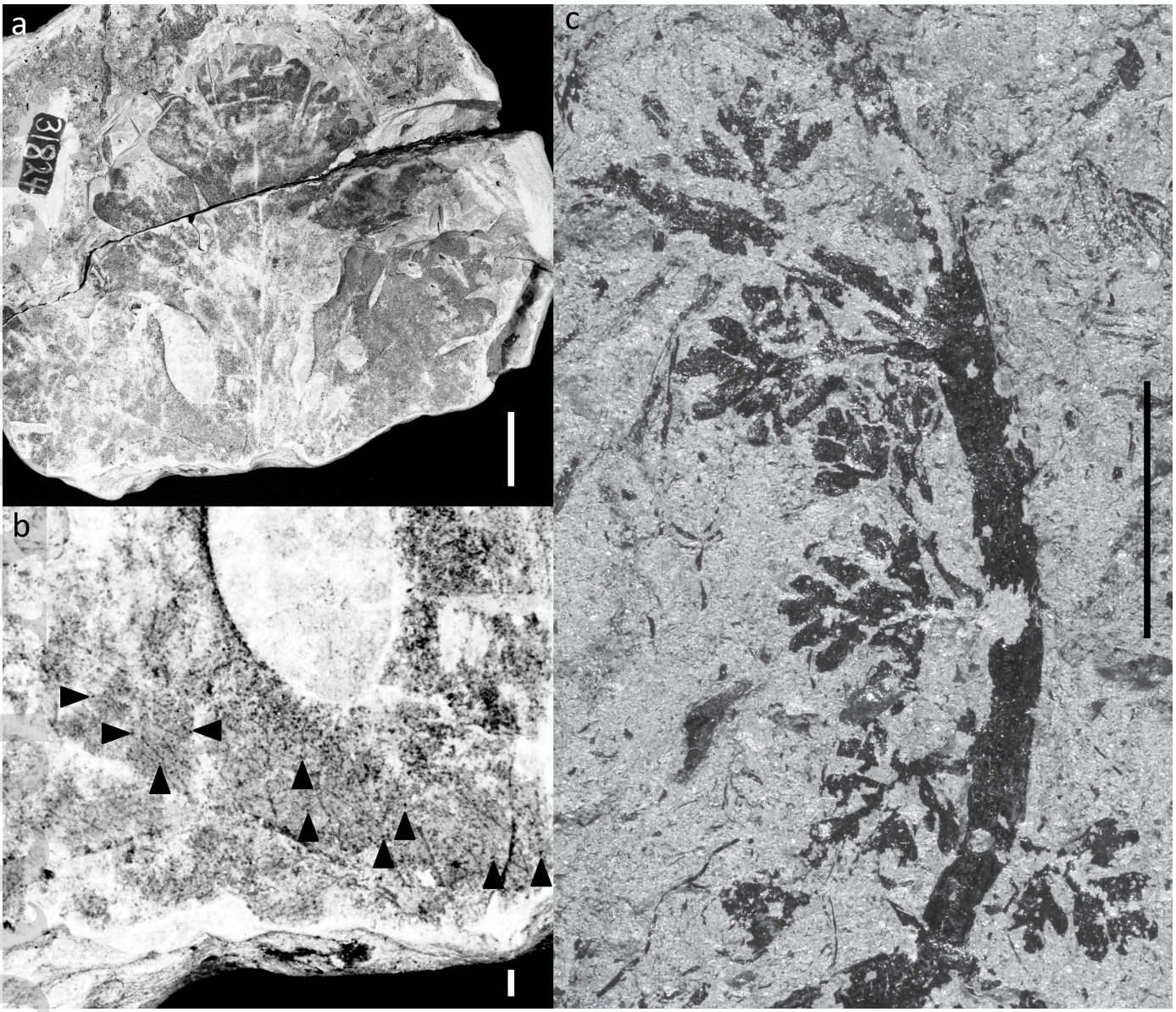

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